Field Observations of Dendraster excentricus, a Sand Dollar of Western North America[1]

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ABSTRACT: Observations were made on behavior, distribution, and biotic relationships of the sand dollar *Dendraster excentricus* along the Pacific coast of California and Baja California, Mexico. Populations occur on sandy bottom in bays, tidal channels, and along the outer coast.

Orientation and feeding behavior, which are related to water movement, vary between populations in the different habitats. In sheltered bays, where there is relatively little water movement, sand dollars remain in shallow water, frequently move, and lie flat on the bottom where they feed on deposited material. In tidal channels and protected areas of the outer coast, habitats with moderate water movement, adults are more stationary, usually are in an inclined position, and feed primarily on suspended material. Density estimates and aggregation values are greatest in these populations. In outer-coast areas consistently exposed to heavy seas, where water movement is greatest, sand dollars are usually buried, and presumably feed on deposited material.

Two types of distribution patterns occur in populations along the protected outer coast. In one type, the populations run parallel to shore as dense bands, and maintain a characteristic pattern that is reformed when disrupted by occasional heavy seas. Usually juveniles are most abundant shoreward, and move seaward with age. The outer margin of these populations is well-defined in 4-12 m of water, and here the largest individuals and greatest densities occur. Most of our observations are of these populations. The other type of distribution is similar, except that it extends into deeper water, and below about 10-15 m; individuals become progressively smaller with depth.

Various other organisms coexist with the sand dollars, many of them using the inclined sand dollars as shelter or a hard substrate. Known predators include fishes, crabs and sea stars. Fouling by the barnacle *Balanus pacificus* also may contribute to sand-dollar mortality. At present, separate taxa for the ecologically different populations of *D. excentricus* are not justified.

INTRODUCTION

Little is known about the ecology of the sand dollar *Dendraster excentricus* (Eschscholtz), despite the fact that it is one of the most abundant macroorganisms off many beaches along the Pacific coast of central North America. *D. excentricus* is endemic to this region, ranging at least from Hecate Straits, central British Columbia (Raymond J. Ghelardi, Nanaimo Marine Station, pers. comm.) to Bahia Almejas, Baja California Sur, Mexico. Although Eschscholtz (1831) gave Unalaska as the type locality, Rathbun (1886) was probably

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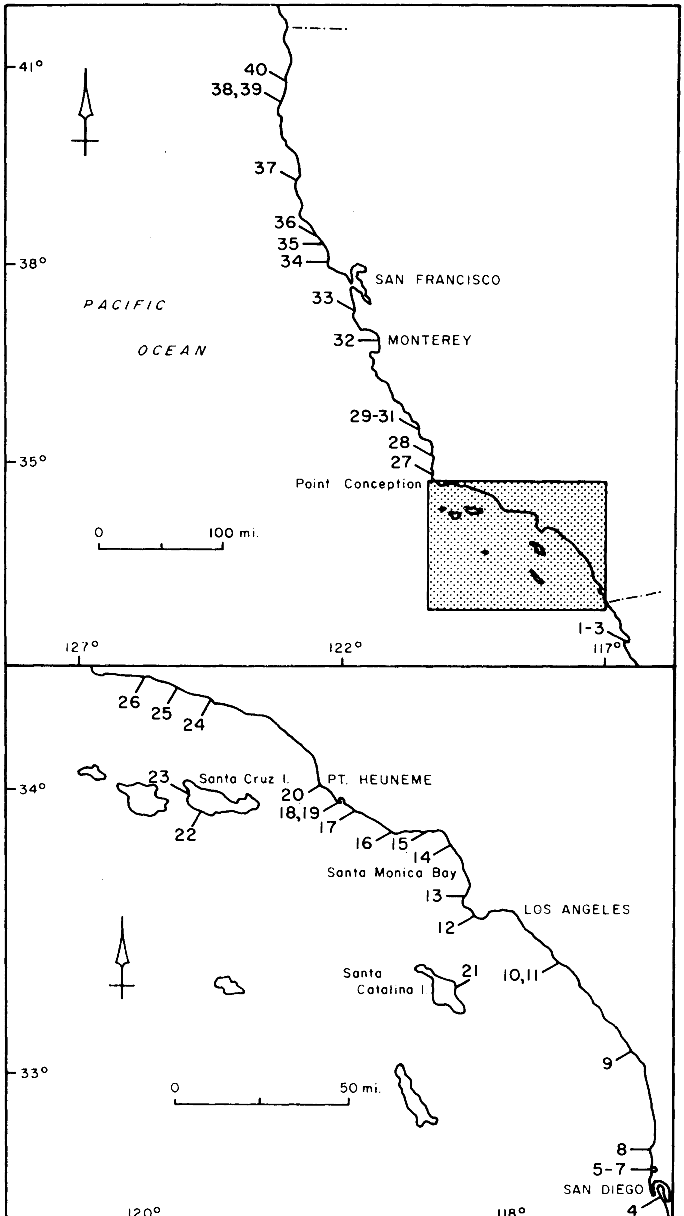

Fig. 1.—Map showing approximate location of principal adult *Dendraster excentricus* populations observed during study. Area in lower section is shown as stippled insert in upper section. Numbers refer to Table 1.

TABLE 1.—Location of adult *Dendraster excentricus* populations investigated during this study: B = Bay; T = Tidal Channel; POC = Protected Outer Coast; EOC = Exposed Outer Coast.

LOCATION NUMBER	HABITAT TYPE	
		MEXICO:
1	B&T	Estero de Punta Banda, Baja California
2	POC[3]	Estero de Punta Banda at Estero entrance
3	POC[1]	Bahia de Todos Santos, Baja California, N of Estero entrance
		CALIFORNIA:
		San Diego County
4	POC[1]	Silver Strand Beach State Park, Coronado
5	B	SW Mission Bay
6	T&POC[3]	Mission Bay entrance channel
7	POC[1]	Mission and Pacific Beaches
8	POC[1, 2]	Offshore of Scripps Institution of Oceanography
9	POC[1]	Area N of Oceanside Pier, Oceanside
		Orange County
10	B	Lower Newport Harbor
11	POC[1, 2]	Laguna and Balboa Beaches
		Los Angeles County
12	POC[1&2]	Vicinity of Marineland Pier, Palos Verdes
13	POC[2]	Malaga Cove, Sànta Monica Bay
14	POC[1]	Inside detached breakwater, Santa Monica
15	POC[1]	Keller's Shelter, Malibu
16	POC[1, 2]	Pt. Dume past Zuma Beach County Park
		Ventura County
17	POC[2]	Immediately E. of Pt. Mugu
18	T	E end of Mugu Lagoon
19	POC[1]	Offshore area from W baymouth bar of Mugu Lagoon
20	POC[1, 2]	Areas on both sides of Port Hueneme entrance channel
		Channel Islands
21	POC[3]	White's Cove, Catalina Island
22	POC[2]	Morse Point to Pt. Arena, Santa Cruz Island
23	POC[3]	Christi Ranch Beach, Santa Cruz Island
		Santa Barbara County
24	POC[3]	Arroyo Burro Beach State Park
25	POC[3]	Ellwood Beach
26	POC[3]	Refugio Beach State Park
27	EOC[1]	Ocean Beach Park, Surf
		San Luis Obispo County
28	EOC[1]	Pismo Beach
29	T	N end of Morro Bay
30	POC[3]	N end of Morro Bay, at Bay entrance
31	EOC[1, 2]	Estero Bay
		Monterey County
32	POC[1, 2]	Monterey Bay
		San Mateo County
33	POC[2]	Half Moon Bay
		Marin County
34	EOC[3]	South Bodega Bay
		Sonoma County
35	POC[3]	Campbell Cove, north Bodega Bay
36	EOC[2]	Salmon Creek Beach
		Mendocino County

correct in doubting the validity of this location; no specimens have been reported north of British Columbia since the original description.

The literature on *Dendraster excentricus* in its natural habitat deals almost exclusively with individuals inhabiting intertidal sand-flats, or the shallow waters of protected inlets (*e.g.*, Johnson and Snook, 1927; Clark, 1935; MacGinitie, 1935; Ricketts and Calvin, 1952; MacGinitie and MacGinitie, 1968). Sand dollars in much larger assemblages, with different patterns of distribution and ecological situations, occur offshore; these have not been studied although, before his death in 1960, Conrad Limbaugh of Scripps Institution of Oceanography (unpublished data), used a scuba to observe *Dendraster* spp. off southern California (see also Trask, 1955).

Between 1963 and 1968 we used diving equipment while studying populations of *Dendraster excentricus* and *Dendraster laevis* at various locations along the Pacific coast between Eureka, California, and Bahia de Todos Santos, Baja California, Mexico (Fig. 1 and Table 1). During this period over 250 hours were spent underwater observing sand dollars. In this paper we describe the distribution and some ecological relationships of *Dendraster excentricus.* The various techniques and equipment used are discussed as they pertain to the report. Unless otherwise defined, oceanographic terms follow definitions of the Beach Erosion Board (1961). The location numbers in parentheses refer to Table 1 and Fig. 1. All references to sand dollars are to *D. excentricus* unless otherwise stated.

MORPHOLOGY AND BEHAVIOR

PERTINENT ASPECTS OF MORPHOLOGY

Like all exocyclic echinoids, *D. excentricus* possesses a secondary bilateral symmetry. The anteroposterior axis runs along a plane passing through the (posterior) periproct, the peristome, the apical system and the anterior margin of the test (see Durham, 1955; Melville and Durham, 1966). Bilateral symmetry, together with a reduction in the length of the spines, is probably an important adaptation to life on a soft substrate (Hyman, 1955).

The four genital pores within the madreporite first appear in *D. excentricus* that are between 12 and 21 mm long. The presence of genital pores is our criterion for distinguishing "adult" from "juvenile" individuals.

Superimposed on these more general skeletal characteristics is a

37	EOC[1]	MacKerricher State Park, Fort Bragg
		Humboldt County
38	B	North Bay Channel, Humboldt Bay
39	EOC[2]	N and S of Humboldt Bay entrance channel
40	EOC[2]	Little River State Park

Population(s):
[1] with abrupt seaward limit to distribution
[2] extending into water deeper than about 40 ft (12.2 m)
[3] small local populations

posterior shift of many surface features of the test (*e.g.*, the petaloids, food grooves, peristome and apical system). The posteriorly eccentric position of the apical system (eccentricity) is one of the principal traits distinguishing *Dendraster* from other living scutellinid genera. The degree of eccentricity is probably related to the sand dollar's unusual habit of maintaining an inclined position with respect to the substrate (Durham, 1955; Raup, 1956).

DISPOSITION AND MOBILITY

Inclined Attitude and Locomotion

The inclined attitude assumed by *D. excentricus* under specific conditions has been described by Clark (1901, 1935) and Mortensen (1921). In this position the anterior end of the animal is inserted into the sand, and the oral surface forms an acute angle with the substrate (Fig. 2). With the exception of *Dendraster laevis* Clark (R. Merrill, in prep.) and the west African rotulids (Dartevelle, 1936), *D. excentricus* is the only clypeasteroid known to maintain an inclined attitude (Mortensen, 1948), although other sand dollars go through upright positions while righting themselves, *e.g.*, *Echinarachnius parma* (Parker, 1927), *Astriclypeus manni* (Ikeda, 1941), *Clypeaster subdepressus, Encope michelini* (Kier and Grant, 1965), and *Mellita quinquiesperforata* (Weihe and Gray, 1968). Although sand dollars can right themselves on smooth sand, the process usually takes several hours, depending on conditions (Chia, 1969). In the field and laboratory *D. excentricus* attains the inclined attitude from the typical horizontal position with the oral surface downward.

When the water is calm, inclined sand dollars occasionally move about; their movement is lateral, in either direction, with the bilateral axis perpendicular to the substrate. Locomotion rates of 18 inclined adults were measured during slack tide in water 2 to 6 ft (0.6 to 1.8 m) deep in Mugu Lagoon (loc. 18). Rates of movement were determined by measuring the narrow trough of sand behind the trailing edge of the inclined test. Measurements were taken at one minute intervals for 15 minutes on individuals averaging 66 mm long (range 51 to 84 mm). The average maximum rate of locomotion for individuals was 3.8 mm/min (range 1.9 to 5.9 mm/min), and the mean of the average rates of locomotion was 3.1 mm/min (range of averages 1.7 to 4.9 mm/min). Consistently faster rates were observed under laboratory conditions. There was a significant positive correlation ($p < .01$) between the size of the individuals and their average range of movement (Spearman coefficient, $r_s = .78$).

Moving while inclined permits mobility within high density aggregations, where movement in the horizontal attitude (see below) might be restricted by the proximity of other individuals.

A description of the inclined behavior is made easier by defining two of its components: (1) the *substrate angle* is the angle between the inclined oral surface of the test and the surface of the substrate, and (2) the *current angle* is the angle between the line of the exposed posterior portion of the test (the ambitus, viewed from above) and the direction of the water current.

Horizontal Attitude and Locomotion

In tranquil water, *D. excentricus* often lies flat, oral side down on, or just below, the surface of the sand. Locomotion in this position is similar to that described for other sand dollars (*e.g.*, Parker and Van Alstyne, 1932; Ikeda, 1939). Two types of locomotion may be distinguished: *progression* and *rotation* (Parker, 1927). Progression is movement parallel to the animal's bilateral axis, with the anterior margin of the test always leading. Also, the animal may simply rotate its test, with the peristome as a pivoting point. Rotation and progression are combined to varying degrees when the sand dollar is changing

Fig. 2.—Patches of adult *Dendraster excentricus* at shoreward portion of protected outer-coast population (Zuma Beach). Note typical inclined position.

the direction of movement or burying. For a more detailed description of locomotion in *D. excentricus* see Chia (1969).

D. excentricus moves more rapidly when horizontal than when inclined. For example, the average rate of progression during a 1-minute interval, as measured for 27 isolated adults (53 to 79 mm long) that were moving on the surface of the sand in 4 to 6 ft (1.2 to 1.8 m) of water in Mission Bay (loc. 5), was 38 mm/min (range 21 to 56 mm/min). Similar values were obtained in other locations: 16 individuals (48 to 71 mm long) from Newport Harbor (loc. 10) averaged 33 mm/min (range 19 to 47 mm/min), and 14 individuals (43 to 58 mm long) from Estero de Punta Banda (loc. 1) averaged 27 mm/min (range 16 to 57 mm/min). These average rates are greater than rates given for other sand dollars: 18 mm/min maximum for *Echinarachnius parma* (Parker, 1927), 11 to 26 mm/min for *Mellita lata* (Kenk, 1944), and 14.6 mm/min average on the sand surface for *Mellita quinquiesperforata* (Weihe and Gray, 1968).

DESCRIPTION OF POPULATIONS

It is convenient to consider the ecology of *D. excentricus* in terms of four subjectively defined habitats that the sand dollar occupies: (1) bay, (2) tidal channel, (3) protected outer coast, (4) exposed outer coast. The first two habitats are referred to as coastal inlets and the latter two as outer coast. The term "population" is used only in the spatial sense referring to assemblages of sand dollars that are relatively isolated from one another.

COASTAL INLET POPULATIONS

Coastal inlets are protected from ocean waves. In most of the harbors, lagoons, sloughs, etc., that we investigated, we found *D. excentricus,* and where it did not occur there are reports that populations existed prior to dredging. For example, large populations were once present in Elkhorn Slough, Monterey Bay (MacGinitie, 1935; Ricketts and Calvin, 1952) and in parts of Newport Harbor, California (Limbaugh, unpubl. data; MacGinitie, 1939) where they have not been found since these areas were dredged.

Isolated individuals and small groups occur throughout many coastal inlets, frequently on sand patches within and near beds of the plant *Zostera* (Shelford *et al.,* 1935; MacGinitie and MacGinitie, 1968, Fig. 101). MacGinitie and MacGinitie (1968) reported that *D. excentricus* inhabits estuaries, referring to individuals in coastal inlets as the "estuarine form." Although many of the coastal inlets that we investigated are, in parts, estuarine, the largest aggregations of *D. excentricus* in these inlets occur near openings to the sea.

Bay Populations

D. excentricus often occurs in harbors with wide entrance channels and in areas of other coastal inlets without strong tidal currents. Here, there is a substrate of fine, poorly sorted sand, usually with an overlying layer of detritus. In this situation most individuals assume a horizontal position on, or just beneath, the surface of the sand.

Observations on the distribution of sand dollars were made in three bays (Estero de Punta Banda, Mission Bay, and Newport Harbor) during neap high tides of late summer (Table 2). To minimize bias, $^1/_9$ m^2 quadrat frames were cast in random directions from the water's surface. Maximum tidal range during the sampling was always less than 0.5 ft (15.2 cm). The data obtained were arrayed in a 4 x 3 (depth x horizontal and sum of inclined dispositions) contingency table. The chi-square value of association between the categories (on actual numbers) is significant ($p < .001$), suggesting a strong relationship between disposition and water depth within a relatively narrow depth zone. The highest proportion of sand dollars occurs in water 2 to 4 ft (0.6 to 1.2 m) deep. Here individuals generally move about haphazardly in the horizontal position. The majority in shallower water also lie flat, but most of these are buried. Few sand dollars occur in water deeper than 6 ft (1.8 m). Other observations showed that sand dollars about to be exposed by falling tides burrow, rather than move to deeper water, even though locomotion rates suggest that such migrations would be possible.

Conditions may become unfavorable when the shallow water is diluted by heavy rains. At such times most sand dollars may remain buried for long periods (see MacGinitie, 1939).

The proportion of inclined sand dollars increases when there are surface waves due to storms or other disturbances. This change in position is notable in Newport Harbor during local winds of early spring and late autumn, and also in Mission Bay when boating is heavy.

Tidal-Channel Populations

In parts of many coastal inlets, especially those with a narrow access to the open sea, strong tidal currents produce channels of clean, well-sorted sand. This habitat frequently supports large populations of *D. excentricus,* with most individuals in the inclined position.

Substrate angles are generally uniform throughout these populations. Maximum angles occur when currents are moderately strong, but when currents increase to their extremes during spring tides there is a noticeable decrease in angle.

Current velocity also influences current angle. Observations were made in Mugu Lagoon and Morro Bay (loc. 29), the latter having markedly stronger currents. Using a specially constructed bezel compass, current angles were measured to the nearest 18° on individuals in randomly placed $^1/_9$ m^2 quadrats. The angle was measured clockwise, where 0° was defined by a sand dollar with its oral surface facing upstream and the observer facing downstream. Current direction within each quadrat was determined using fluorescent dye. All measurements were made during the ebb of spring tides. We analyzed the current angle distributions (Fig. 3) using the methods discussed

TABLE 2.—Disposition and depth distribution of individuals in three populations of *Dendraster excentricus* in bays. E = Estero de Punta Banda (n = 155), M = Mission Bay (n = 197), N = Newport Harbor (n = 391). Values are proportions. For each disposition within each depth category the proportion is that of all individuals (all depths) from the designated locality. Also given: *depth total/location* = the proportion of all individuals from each of the three localities in each depth category; *grand depth total* = the proportion of all individuals from all three depth category; and *disposition total* = the proportion of all individuals from all three localities in each disposition.

Depth in ft (m)	Location	Inclined: Still	Inclined: Moving	Buried	Horizontal: Exposed & still	Horizontal: Exposed & moving	Depth total/ location	Grand depth total
⩽2.0 (0.6 m)	E	......	......	.142	0.19	.032	.193	
	M	.010	......	.096	.041	.010	.157	.215
	N	.031	.005	.159	.043	.015	.253	
2.1 to 4.0 (0.6 to 1.2 m)	E	......	......	.039	.136	.464	.639	
	M	.061	.015	.035	.061	.345	.518	.572
	N	.146	.023	.031	.118	.253	.570	
4.1 to 6.0 (1.2 to 1.8 m)	E	......	......	.039	.052	.077	.168	
	M	......	......	.046	.041	.157	.244	.183
	N	.008	......	.021	.005	.125	.159	
⩾6.1 (1.8 m)	M	......	......	.010	......	.071	.081	
	N	......	......	.010	.003	.005	.018	
Disposition Total		.089	.019	.211	.170	.511		1.000

by Batschelet (1965). The two distributions are neither random (uniformly distributed) nor normal (X^2 tests, $p<.001$), but they are significantly different ($X^2= 75$, $p<.001$). Basically the difference is in variability among individuals, rather than between the mean current angles of the populations.

Both distributions show three predominant current angles—in one the upright test is roughly perpendicular to the current, with the mouth facing upstream, and in the other two the test is parallel to the current, with the mouth facing either right, or left, across the current. At Morro Bay the frequency of these three current angles was similar. However, in Mugu Lagoon, where the current was weaker, most sand dollars were oriented with the mouth facing upstream.

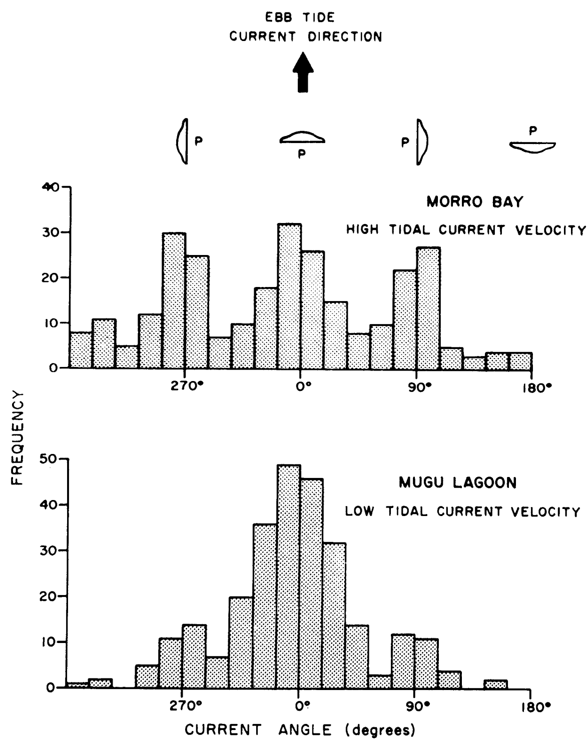

Fig. 3.—Distribution of the current angles of individuals in two tidal-channel populations of *Dendraster excentricus:* Morro Bay (loc. 29) and Mugu Lagoon (loc. 18). The four diagrammatic figures along the top represent sand dollars (viewed from above) oriented to the current direction (arrow) in the same way as individuals represented by that part of the graph below each figure. P = position of peristome. Frequency = number of sand dollars.

OUTER-COAST POPULATIONS

Extensive populations of *D. excentricus* live on the sand bottom just seaward of the breaker line off many beaches, where currents are caused by wave surge and where sediment is being continually deposited and eroded (Eagleson *et al.*, 1961).

Effects of sand deposition and erosion.—The distribution of nearshore sand strongly influences, directly or indirectly, the size of sand-dollar populations. In southern California, longshore drift is predominantly southeastward, and sand frequently accumulates on the north or west side of jetties (Johnson, 1956; Emery, 1960). Sand-dollar populations immediately updrift of the jetties are generally more extensive than those farther updrift (loc. 7, 11, 20). On the downdrift sides of jetties, populations are usually very small, sometimes comprising only a few individuals (loc. 11, 20).

In Santa Monica Bay (loc. 14) a detached breakwater has modified the inshore current system so that a large deposit of sand has accumulated (Handin and Ludwick, 1956). This deposit supports one of the few large sand-dollar populations in the bay.

Aggregations near the heads of at least some submarine canyons (*e.g.*, La Jolla, Redondo, Dume, and Mugu Canyons) exhibit fluctuations in size and density not noticed elsewhere. For example, at least twice since early 1965 the population at the head of Mugu Canyon (loc. 19) has become re-established after having almost completely disappeared. We found sand dollars in canyons to depths of 120 ft (36.6 m), and they were usually moving back up the sand slides at the canyon head toward shallower water. Thus it appears that sand dollars are at least occasionally carried into the canyons with sliding sediments.

Wave surge.—The coastline south of Point Conception, and certain locations to the north that are protected by local topographic features, are here termed protected outer coast. The remainder of the coastline north of Point Conception is here termed exposed outer coast. The coastline north of Point Conception includes what is essentially a subtidal extension of the "protected outer coast" and "open coast" of Ricketts and Calvin (1952), who used these terms to characterize the shoreline of this region on the basis of wave shock. Off southern California protection is provided by the presence of offshore islands and by the configuration of the coast (Fig. 1).

Protected Outer-Coast Populations

Along the outer coast, sand dollars south of Point Conception usually maintain the inclined positions, with their test parallel to the strong onshore-offshore sweep of the surge, and perpendicular to the weaker currents moving parallel to shore (Fig. 4). However, these less conspicuous alongshore currents may also influence orientation, as there is a significant tendency for the sand dollars to orient with their oral surface facing upcurrent. We cast $^{1}/_{9}\,m^2$ quadrats from the water surface to get unbiased estimates (see Fager *et al.*, 1966).

At five locations, 1878 of the 2959 inclined individuals sampled had their oral surface facing into the prevailing nearshore current moving parallel to shore (X^2 test, $p<.001$): 64.2% ($n = 1036$, $p<.001$) near Marineland Pier (loc. 12); 70.2% ($n = 427$, $p<.001$) at Mission Beach (loc. 7); and 55.3% ($n = 544$, $.05>p>.01$) at Malaga Cove (loc. 13). Although the sand dollars tended to have their mouths facing upcurrent, within 86.2% of the total quadrats there was a significantly ($p<.05$) greater number of sand dollars facing in one direction—either upcurrent or downcurrent. Under normal sea conditions, fewer than 5% of the large adults (>50 mm long) in these populations were completely buried, and less than 0.4% were horizontal on the sand surface.

Along the protected outer coast, some populations are restricted to the nearshore region, and have a sharp, well-defined seaward limit in 15 to 40 ft (4.6 to 12.2 m) of water. Other populations are not restricted to the nearshore region, but extend into deeper water.

Populations with a sharp seaward margin.—Many large populations along the protected outer coast are distributed in a large band that follows an irregular course roughly parallel to shore. The Zuma Beach population is typical of such a distribution. The bed extends for more than 3 miles (5.8 km) northwest from a rocky headland, Point Dume, and ranges in width from 300 ft (91.4 m) at Point Dume, to less than 50 ft (15.2 m) at its northwest extremity. From its abrupt seaward margin in 20 to 40 ft (6.1 to 12.2 m) of water, the population extends shoreward to the vicinity of the low spring tide breaker line, where the limit of distribution is not distinct.

The sand dollars nearest the beach are mostly small juveniles

Fig. 4.—View from above of sand dollars in a population along the protected outer coast (Zuma Beach), showing uniform posture of inclined individuals with their test parallel to the surge current (up and down the figure).

(< 10 mm long) that are buried in the sand. Seaward from here the individuals become progressively larger, and increasingly tend to assume the inclined attitude. Over the same area isolated large adults (> 50 mm long) are scattered about in the inclined position, frequently with small adults (25 to 50 mm long) clustered around them. Continuing seaward, there are more large adults in these clusters, better described now as patches, separated by areas of open sand (Fig. 2). Still farther offshore, the isolated patches are increasingly extensive until they coalesce, and the bottom is covered with large inclined adults (Fig. 4). This point is about 150 ft (45.7 m) from the shoreward limit of the population. The density continues to increase slightly offshore, and is maximum at the sharp seaward margin of the population (Fig. 5).

Variations from this typical distribution pattern usually depend upon sea conditions. When the sea is calm, sand dollars near the seaward edge of the population move toward the beach resulting in an onshore shift of the seaward margin and an increase in the density of individuals in the seaward segment of the population. During extended periods of calm seas the sand dollars are piled on top of one another to create exceptionally high densities (Fig. 6). We did not

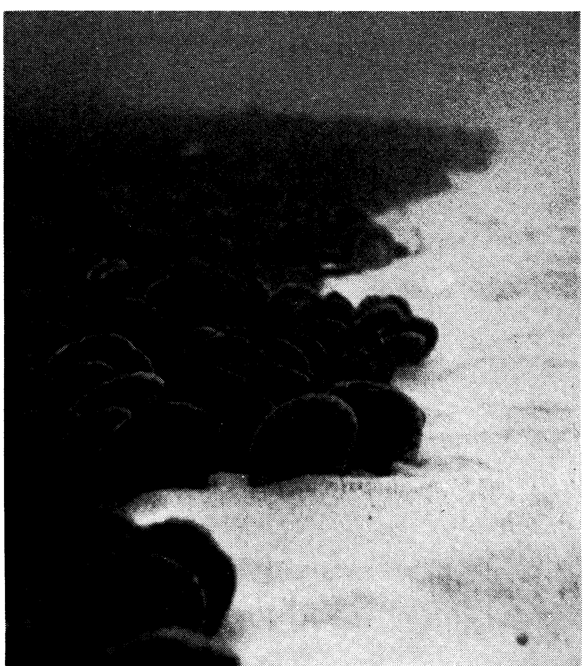

Fig. 5.—The typical seaward margin of a population along the protected outer coast (Zuma Beach). Shore is to the left in the figure.

notice changes in the shoreward segment of the population under these conditions. When the sea is rough, the sharp outer margin disappears as many individuals move, or perhaps are carried, as much as 50 m seaward. Others are washed ashore due to factors discussed below. Under high seas, sand dollars have a low substrate angle or are buried in the sand (Fig. 7).

There appears to be a relationship between the general wave climate of a particular area and the shoreward limit of the sand-dollar population in that area. Where local features often produce calm seas, and a more shoreward breaker line, populations lie relatively close to the beach in shallow water (*e.g.,* loc. 3, 12, 14, 15). Where there is more exposure to wave action, and the breaker line is farther offshore, the population lies more seaward. We have never seen a seaward margin in water deeper than 40 ft (12.2 m).

Factors controlling the general distribution pattern described above remain unclear. Particularly intriguing is the manner in which a population is reorganized after having been disrupted by storm waves, and the problem of how the distant seaward margin is maintained between disturbances.

Populations extending farther offshore.—Some other populations along the protected outer coast do not have an abrupt seaward margin; instead, they continue seaward for an undetermined distance. We have followed their distribution for up to 1200 m from the beach without finding a limit. On the other hand, we have always been able to observe the offshore limit of populations with a distinct margin,

Fig. 6.—"Pile-on" effect of *Dendraster excentricus* at seaward portion of a population along the protected outer coast (Zuma Beach). Crab is *Loxorhyncus grandis.*

even when they were dispersed by heavy surf. This type of distribution is most common on the downcurrent side of coastal indentations and rocky headlands; it seems to be associated with a substrate of gradually decreasing particle size.

The inshore distribution pattern is similar to that of populations with a sharp seaward margin. However, as the population continues into deeper water, individuals noticeably decrease in size (Fig. 8); and, in contrast to the uniform ranks of the larger sand dollars inshore, become oriented haphazardly in different directions.

Exposed Outer-Coast Populations

Many beaches along the coast north of Point Conception are characterized by a low shoreface profile and a wide surf zone with several breaker lines relatively far offshore. Here sand dollars are not as close to shore as they are off southern California.

Most sand dollars that we observed off the exposed beaches were completely buried. Similarly, R. J. Ghelardi (pers. comm.), during frequent observations at Salmon Creek Beach (loc. 36), has never seen large numbers of sand dollars in the uncovered, inclined position. But in sheltered water 3 miles (4.8 km) south (loc. 35), we found most sand dollars uncovered and inclined.

Orientation of sand dollars off the exposed beaches resembles that of sand dollars off the protected outer coast during heavy seas. Individuals are variably inclined under the sand, with the lateral axis parallel to the surge. In high density they overlap one another like

Fig. 7.—A hornyhead turbot, *Pleuronichthys verticalis,* lying among sand dollars that have been scattered and partially covered by a local storm. Zuma Beach.

shingles on a roof. When the sea is suitably calm, sand dollars off exposed beaches probably assume the inclined position on the sand surface; but we made no observations here under such conditions.

The distribution of these populations can also be described as either ending abruptly in relatively shallow water (*e.g.*, Rechnitzer and Limbaugh, 1959), or extending for an undetermined distance offshore.

The exposed outer-coast situation apparently extends north from Point Conception into Oregon and Washington. Since we have concentrated attention on populations off the comparatively protected southern California coastline, we know relatively little about populations that live under other conditions.

DENSITY AND DISTRIBUTION PATTERNS

Population Density

The population density of adults was estimated in certain locations along with some characteristics of water movement. We used $^1/_9$ m^2 quadrats to sample selected populations from the four habitat types. In coastal inlets, counts were made of adults within quadrats placed at random or cast haphazardly from randomly placed positions within the populations. Outer-coast populations were sampled at regular intervals along parallel transects perpendicular to shore. At most locations replicate collections were made under a variety of field conditions, and the data were pooled for analysis. However, the Zuma Beach collections were made at the same site during calm, "normal," and heavy surge, and the data from each collection were analyzed separately.

These data (Table 3) indicate that the average densities of adult populations are lowest in the bay habitat, highest in the tidal channel and protected outer-coast habitats, and intermediate for exposed

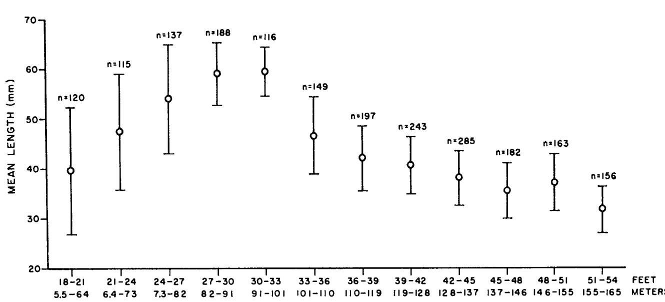

Fig. 8.—The mean size (± 1 s.d.) of adult sand dollars in an extended outer-coast population (loc. 17) in relation to water depth. Data for each depth range are from 2-10 1/9 m^2 quadrats (115-285 individuals). Numbers of individuals sampled in each depth range are given above vertical s.d. lines. These numbers do not reflect density, but rather number of quadrats in each depth range.

outer-coast populations. At Zuma Beach we found an inverse relationship between density and the width of the colony. This is due primarily to the fact that, during heavy seas much of the population is dispersed seaward from its normally abrupt seaward limit of distribution, but when the sea is calm individuals in the seaward part of the colony move shoreward.

Patterns of Distribution in Coastal Inlets

Data gathered for the density estimates were used to analyze the distribution patterns of some populations in coastal inlets. These patterns were consistently nonrandom (aggregated). The coefficient of dis-

TABLE 3.—Maximum and mean density (± 1 s.e.) of adult *Dendraster excentricus* populations from the different habitats. Q = no. of quadrats in sample. Also given for coastal inlet populations are p, the probability that the coefficient of dispersion equals unity, and "patchiness" (Lloyd, 1967) with ± 1 s.e.

Location	Q	Max. den./m²	Avg. den./m²	
	Bays			
Estero de Punta Banda	52	45	11 ± 2	
Mission Bay	54	63	16 ± 2	
Newport Harbor	70	153	31 ± 4	
	Tidal Channels			
Mission Bay Entr. Chan.	62	684	114 ± 24	
Mugu Lagoon	92	414	83 ± 13	
Morro Bay	104	513	87 ± 13	
	Protected Outer Coast			*Width of Population*
Mission Beach	43	630	246 ± 40	
Oceanside	47	666	230 ± 36	
Santa Monica Pier	84	1386	467 ± 51	
Zuma Beach	80[a]	1026	375 ± 36	260 ft (79.2 m)
	63[b]	747	310 ± 30	280 ft (85.3 m)
	37[c]	423	140 ± 19	560 ft (170.7 m)
E of Pt. Mugu	53	1044	348 ± 30	
South Monterey Bay	32	396	159 ± 28	
	Exposed Outer Coast			
Pismo Beach	50	288	62 ± 10	
Estero Bay	47	198	51 ± 7	
Salmon Creek Beach	39	144	34 ± 6	

Data collected at site during: [a]calm, [b]"normal," and [c]rough sea conditions.

TABLE 3.—(continued)

Location	p	"patchiness"
	Bays	
Estero de Punta Banda	$.05 > p > .025$	1.14 ± 0.19
Mission Bay	$.025 > p > .01$	1.27 ± 0.18
Newport Harbor	$p < .001$	1.78 ± 0.24
	Tidal Channels	
Mission Bay Entr. Chan.	$p << .001$	3.78 ± 1.01
Mugu Lagoon	$p << .001$	3.15 ± 0.58
Morro Bay	$p << .001$	3.40 ± 0.62

persion (ratio of variance to mean) for each population was significantly ($p = .05$) greater than one (Table 3), as judged statistically by $X^2 = (Q - 1)\ s^2/x$ with $(Q - 1)$ degrees of freedom, where $Q =$ number of quadrats (Fisher, 1958).

Although the coefficient of dispersion is useful as a test of aggregation, it is not a good measure of the degree to which organisms are aggregated. With increasing aggregation the variance and mean of the density distribution are not linearly related. Thus the coefficient is not an accurate measure of the extent of crowding that an individual experiences.

As a measure of the degree of aggregation in natural populations, Lloyd (1967) proposed an index that he termed "patchiness." Patchiness ($\overset{*}{m}/m$) is equal to one plus the reciprocal of the negative binomial parameter k, and purports to measure how many times as "crowded" an individual is, on the average, as it would be if the same population had a random distribution. As an index of dispersion, therefore, $\overset{*}{m}/m$ is both intuitively and ecologically appealing. For the purposes of this paper, sample estimates of $\overset{*}{m}/m$ are based on moment estimates of k.

The values of $\overset{*}{m}/m$ obtained by applying Lloyd's methods to our data (Table 3) indicate that sand dollars in tidal channels are approximately 3.5 times as crowded as they would be if they were distributed at random, whereas those in bays were only about 1.5 times as crowded as they would be if distributed randomly.

Within quadrats in outer-coast populations, inclined sand dollars are distributed uniformly (Fig. 4). We analyzed the distribution pattern within quadrats of horizontal sand dollars in bays using the method of distance to nearest neighbor (Clark and Evans, 1954), but could find no consistent pattern to the distribution.

Associated Organisms

A wide variety of animals live in association with populations of *D. excentricus* along the outer coast. We found no animals endemic to sand-dollar beds, but many organisms are recurrent and can be regarded as characteristic of the beds.

Table 4 lists animals that we frequently observed in outer-coast sand-dollar beds south of Point Conception. Some of the fauna that we found associated with sand dollars north of Point Conception were listed by Rechnitzer and Limbaugh (1959).

SPECIES INTERACTIONS IN SAND-DOLLAR BEDS

Many animals seem to find advantage living in sand-dollar beds. Some of the relationships with sand dollars may be more direct than others. Described below are some examples taken from outer-coast populations off southern California. The material is arranged in categories that have been erected for convenience in presentation only.

Direct Relationships with Sand Dollars

Sand dollars as a substrate.—The sand dollars themselves are used as a substrate by some organisms. The fouling of *D. excentricus* by the barnacle *Balanus pacificus* has been described (Giltay, 1934; Boolootian, 1964). MacGinitie (1935) identified barnacles on *D. excentricus* from Monterey, California, as *B. tintinnabulum californicus*. *B. t. californicus*, as well as *B. pacificus*, occurs on rocks, gastropods, large crabs, and other hard surfaces within sand-dollar beds, but we have seen only *B. pacificus* on sand dollars. We found this barnacle on *D. excentricus* in most outer-coast populations from

TABLE 4.—Organisms frequently associated with outer-coast sand-dollar populations south of Point Conception. *** = abundant in sand-dollar beds but not in areas surrounding beds; ** = abundant in beds and also abundant in areas surrounding beds; * = occur in some beds and surrounding areas.

COELENTERATA	
* *Cerianthus* sp.	
*** *Clytia bakeri*	
* *Edwardsiella californica*	
** *Renilla kollikeri*	
* *Stylatula elongata*	
MOLLUSCA	
Gastropoda	
*** *Balcis rutila*	
* *Bursa californica*	
* *Conus californica*	
* *Kellettia kellettii*	
** *Nassarius fossatus*	
** *N. perpinguis*	
* *N. tegulus*	
* *Olivella baetica*	
** *O. biplicata*	
* *Pleurophyllidia californica*	
** *Polinices altus*	
* *P. draconus*	
** *P. lewisii*	
* *P. recluzianus*	
Pelecypoda	
** *Tivela stultorum*	
ANNELIDA	
* *Chaetopterus variopedatus*	
* *Nephtys* sp.	
several unidentified species	
CRUSTACEA	
Cirripedia	
*** *Balanus pacificus*	
* *B. tinntinabulum californicus*	
Peracarida	
*** *Diastylopsis tenuis*	
*** *Mysidopsis* sp.	
*** *Paraphoxus* sp.	
Anomura	
** *Blepharipoda occidentalis*	
** *Holopagurus pilosus*	
* *Pagurus ochotensis*	
* *Paguristes ulreyi*	
Caridea	
*** *Hippolyte californiensis* (juv.)	
Brachyura	
*** *Cancer* spp. (especially juv.)	
*** *Heterocrypta occidentalis*	
* *Loxorhynchus crispatus*	
** *L. grandis*	
*** *Portunus xantusii*	
*** *Randallia ornata*	
ECHINODERMATA	
Asteroidea	
** *Astropecten brasiliensis armatus*	
* *A. verrilii*	
* *Patiria miniata*	
* *Petalaster foliolata*	
* *Pisaster brevispinus*	
Echinoidea	
* *Dendraster laevis*	
* *Lovenia cordiformis*	
Holothuroidea	
** *Molpadia avenicola*	
FISHES	
** *Citharichthys* sp.	
*** *Neoclinus blanchardi*	
*** *Paralabrax clathratus*	
*** *Pleuronichthys verticalis*	
*** *Sebastodes* spp. (juv.)	
*** *Symphurus atricauda*	

Bodega Bay south to Ensenada, Mexico. *B. pacificus* rarely occurs in coastal inlets (William Newmann, Scripps Institution of Oceanography, pers. comm.).

In many sand-dollar populations the incidence of fouling is high (15% to 25% of adults), and most live sand dollars washed ashore during heavy seas and, especially, long-period swell, have attached barnacles. This suggests that fouled sand dollars stand an increased chance of being washed ashore. If so, and assuming that most beached individuals cannot return to the offshore population, barnacle-fouling would be a factor in sand-dollar mortality. To check this possibility, we sampled the Zuma Beach population during a period of ocean calm and again just after a local winter storm.

The data obtained (Fig. 9) strongly sugggest that fouled sand dollars tend to be washed ashore more often than those without barnacles, especially during rough seas. The proportion of fouled sand dollars increased shoreward both calm and post-storm periods, but the proportion inshore was much greater after the storm, when there was also a large number of sand dollars stranded on the beach.

In all populations the great majority of fouled sand dollars are adults, probably because they are more often uncovered. Moreover, large adults tend to have larger and disproportionately more barnacles than do small adults. Thus if barnacle-fouling increases the tendency for shoreward transport, one would expect larger sand dollars to be especially vulnerable: during both periods, fouled sand dollars were greater in size (Welch t-test, $p < .01$) than unfouled sand dollars in each of the two shoreward segments of the population, *i.e.*, depths of 18 to 21 ft (5.5 to 6.4 m) and 21 to 24 ft (6.4 to 7.3 m). Furthermore, following the storm, the mean size of fouled sand dollars was greater than during the calm period, and those stranded on the beach were of a maximum size. We obtained results similar to those described above at Pismo Beach and Estero Bay (loc. 31).

The reason for this shoreward transport remains unclear. Perhaps sand dollars with barnacles suffer hydrodynamic problems, or are prevented from burying effectively. Also, barnacles may tend to settle on sand dollars already weakened by disease or injury (especially to the epidermis) or on those in the seaward portion of the population.

Fouling of sand dollars is increased when the barnacles themselves become substrates for such organisms as bryozoans, algae and, especially, the hyroid *Clytia bakeri* (see Giltay, 1934: Fig. 2). In addition, algae sometimes grow directly on sand-dollar tests where the epidermis has been damaged.

In a few outer-coast populations south of Point Conception we have seen a eulimid gastropod, *Balcis rutila,* attached to adult sand dollars. Incidence of attachment is particularly high during late spring in the seaward portion of the populations.

The kelp bass, *Paralabrax clathratus,* a frequent visitor to the beds, utilizes *D. excentricus* quite differently. This fish scrapes its

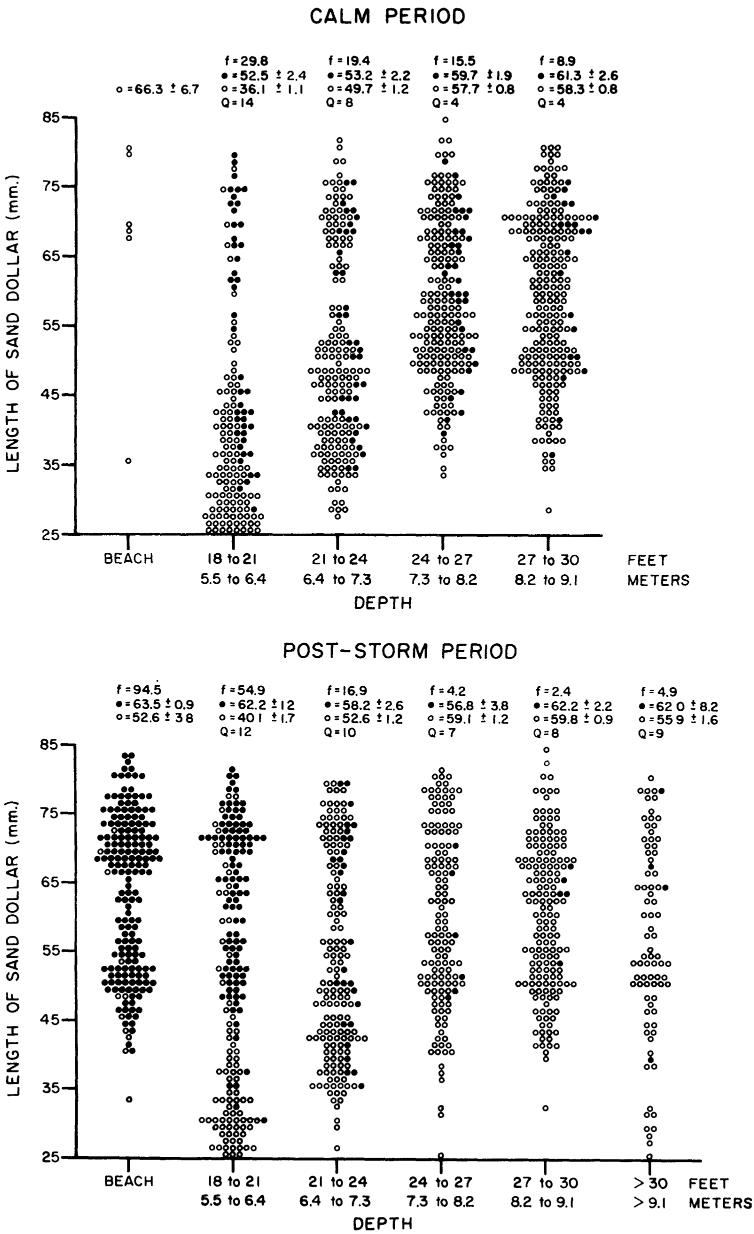

Fig. 9.—Size distribution of adult *Dendraster excentricus* at Zuma Beach. Upper: during calm seas. Lower: after a storm. Each circle represents one sand dollar. • = sand dollar fouled by the barnacle *Balanus pacificus*, ○ =

sides on the abrasive edges of the inclined sand dollars, probably to dislodge ectoparasites or other deleterious material.

Predation on sand dollars.—Sand dollars are prey for a few animals, including some large crabs, sea stars, and fishes.

Many sand dollars in open-coast populations have pieces missing from the edge of their tests (see MacGinitie and MacGinitie, 1968: Fig. 130). We have seen the crabs *Loxorhynchus grandis* (Fig. 6) and *Cancer* spp. feeding on the edge of sand dollars. Nevertheless, as this part of the test is readily regenerated, *D. excentricus* may survive such damage. MacGinitie and MacGinitie (1968) concluded that the spiny lobster, *Panulirus interruptus,* obtains added calcium needed during regeneration and molting by feeding on sand dollars.

Astropecten braziliensis armatus is the most active asteroid predator on sand dollars. *A. b. armatus* seems to feed mostly at night. Other sea stars that we have seen ingesting entire live sand dollars include *Pisaster brevispinus* (also reported by MacGinitie and MacGinitie, 1968, and by Farmanfarmian *et al.,* 1958; Fig. 6), *Pisaster ochraceus,* and *Patiria miniata.*

MacGinitie and MacGinitie (1968: Figs. 89 and 90) reported that when *Pisaster brevispinus* is placed within an aggregation of *D. excentricus* in the field, sand dollars bury themselves as an escape response. Farmanfarmian *et al.* (1958) observed the same phenomenon in aquaria. We attempted to duplicate these observations in Mugu Lagoon using all four asteroid species listed above, but detected no escape response. In contrast to the above-cited escape response, MacGinitie and MacGinitie (1968: p. 226) stated: "*Astropecten armatus* (= *A. braziliensis armatus*), which does not feed on sand dollars, may pass through the same sand dollar bed without disturbing them." Although the MacGinities did not regard *A. b. armatus* as a predator on *D. excentricus* our observations are supported by Hopkins and Crozier (1966) and Fager (1968), who also saw *A. b. armatus* feeding on this sand dollar in the field.

Several fishes feed on sand dollars. Limbaugh (1955) reported *D. excentricus* in the stomachs of pile perch, *Rhacochilus vacca,* and sheepshead, *Pimelometopon pulchrum.* When moving close to shore near Ventura during the breeding season, the larger barred surf perch, *Amphistichus argenteus,* frequently feeds on sand dollars.

Indirect Relationships with Sand Dollars

Habitat modification.—Some organisms may occur in sand-dollar beds because conditions there are more stable than in the surrounding area. On soft bottoms in shallow seas, conditions are harsh due to the

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unfouled sand dollar. Also given for each depth range are (at top of columns): (1) f, the per cent of fouled sand dollars, (2) the mean length ($\pm$ 1 s.e.) of individuals with and without barnacles (• and °); (3) Q, the number of quadrats (1/9 m^2) taken. Beached sand dollars were collected from a 250-ft stretch of intertidal beach shoreward of the offshore sampling sites.

lack of protection and the unconsolidated substrate (Thorson, 1957). These conditions are alleviated by large sand-dollar beds, which provide protection and afford the sandy substrate some degree of consolidation by curtailing, to some extent, erosion of sand. Small eddy systems that occur among inclined sand dollars may facilitate feeding on suspended material. This could be important, not only to *D. excentricus* itself, but also to other animals that feed on material in suspension.

Large populations of sand dollars increase the complexity of the environment over relatively large areas. For example, the Zuma Beach bed, grossly estimated to include over 100 million adult sand dollars, is approximately 3.5 miles (5.6 km) long and, on the average, 190 ft (57.9 m) wide.

Shelter from predators.—Many small animals probably find shelter from predators among the inclined sand dollars. Various juvenile crabs, notably *Cancer* spp. and *Loxorynchus* spp., are abundant in the beds. James A. Macnab (Portland State College, pers. comm.) suggested that sand-dollar colonies are nursery grounds for *Cancer magister* off Coos Bay, Oregon. Many other small crustaceans occur among the sand dollars in far greater numbers than they occur over the surrounding open bottom. These include the cumacean, *Diastylopis tennuis;* a gammarid amphipod, *Parahoxus* sp.; a benthic mysid, *Mysidopsis* sp.; and a few carid shrimps. During late spring, large numbers of juvenile rockfish, *Sebastodes* spp., are sheltered within the Zuma Beach population.

These and other small animals probably help attract the larger predators that occur in the beds. The kelp bass, *Paralabrax clathratus,* was mentioned above. More frequently seen is the hornyhead turbot, *Pleuronichtys verticalis* (Fig. 7), which usually lies partly concealed under the sand in open areas within the beds.

Several smaller fishes that frequently occur among sand dollars can probably be regarded as either predator or prey, depending on the circumstances. Included here is a sanddab, *Citharichthys* sp., the tonguefish, *Symphurus attricauda,* and the blenny, *Neoclinus blanchardi.* On several occasions we have seen the blenny venture out over the open sand several yards away from the sand dollars, then return rapidly to the bed as we approached.

General Remarks

effects of relative water movement

Effect of Water Movement on Feeding Behavior and Orientation

D. excentricus is microphagous. Gut contents invariably consist of small sand grains, diatoms and detritus (Reisman, 1965; Chia, 1969) which are conveyed primarily along the food groove system to the mouth by mucoid-ciliary action of the spines and accessory tube feet. Other scutellinids feed in a similar manner (Goodbody, 1960; Sokolova and Kusnetzov, 1960; Savilov, 1961), but apparently they are exclusively deposit-feeders. *D. excentricus* seems to have morphological and behavioral adaptations for taking suspended material as well. The food grooves, which radiate from the mouth, are posteriorly eccentric and thus more extensively developed on that part of the test that is exposed when the animal is inclined. Furthermore, these grooves extend onto the aboral surface of the test.

The fact that sand dollars assume the inclined position in areas with moderate water movement is probably related to the high amount of suspended material that this condition produces over sand bottoms. One would expect suspended material to be taken more effectively by sand dollars in the inclined position, in which more body surface is in contact with the surrounding water, than by sand dollars that are flat on the bottom or buried. There may also be an advantage in remaining stationary when feeding in that less energy is expended.

Our data from tidal channels indicate that water movement influences both the feeding behavior and the orientation of *D. excentricus.* Sand dollars may find advantage with their oral surface facing upcurrent, a move that probably increases the efficiency with which they receive suspended material. On the other hand, and quite in conflict with the above, it is probably advantageous for sand dollars to position their test parallel to the direction of water movement, thus minimizing the body-surface area confronting the current, and reducing the tendency to be carried downstream. If indeed these two conflicting reactions to current are operating, one would expect sand dollars to position themselves with their oral surface upstream where current is minimal, but, as current velocity increases, to orient, increasingly, parallel to the direction of water flow and the problem of maintaining station becomes critical. Current-angle data from tidal channels (Fig. 4) are consistent with this idea.

On the other hand, MacGinitie and MacGinitie (1968), without providing data, noted that *D. excentricus* tends to orient across the tidal current, but claimed that there is no tendency for the mouth to be facing upstream. Furthermore, Chia (1969) noted that animals in a population at Alki Point, Seattle, Washington, oriented randomly to the tidal current. Possibly, relative differences between the magnitude of ebb and flood tides in different locations contribute to this contradiction.

Sand dollars of the outer coast are similarly affected by water movement. Adults just outside the breaker line orient parallel to the strong sweep of the surge, but tend to have their mouths facing into the less apparent currents running along the shore—at least in protected areas. The less uniform orientation of animals farther offshore probably reflects the decrease in wave-associated water movement in deeper water. In heavy surge, sand dollars are completely buried in the sand, where they presumably feed on deposited material.

We have no direct evidence that *D. excentricus* has a rheotaxic response. It may be that unfavorably oriented animals are passively repositioned by strong currents, or that they are buried as a result of bottom turbulence.

Effect of Water Movement on Population Density and Distribution

Density estimates of adult populations are minimum in areas with much or little water movement and maximum in areas where water movement is moderate—the optimum situation for suspension feeding. Other meaningful parameters remain to be studied. For example, Buchanan (1966) showed that both growth rate and reproductive capacity of the heart urchin, *Echinocardium cordatum,* were greater intertidally than offshore, even though the density of the offshore population was as much as four times greater than that of the littoral population.

At Zuma Beach, the decrease in density when surge is heavy reflects changes in the areal distribution of the population more than fluctuation in the numbers of sand dollars. Dispersal during storms, and subsequent reaggregation during calm seas, have been observed in other large invertebrates inhabiting the nearshore sandy bottoms off southern California (Merrill, 1967).

Sand dollars feeding on suspended material are aggregated, even in what seems to be a homogeneous environment (*e.g.,* the shoreward portion of some outer-coast populations). Nevertheless, inclined sand dollars are usually distributed uniformly within quadrats. Connell (1963) concluded that suspension-feeders among some marine invertebrates space themselves uniformly whenever their feeding brings them in contact with one another. The uniform distribution of sand dollars strongly suggests some avoidance between individuals, although the "pile-on" effect is not consistent with this view.

Aggregations may enhance the mixing of gametes. In addition, as noted above, eddies of suspended material circulate slowly among closely packed sand dollars and thus are retained close to the animal, perhaps facilitating feeding.

The dense concentrations of *D. excentricus* usually located in or near rocky headlands, the entrances of bays, or at the heads of submarine canyons might be related to the presence of accelerated currents with heavy loads of suspended material that are frequently found in these areas. On the other hand, we found mostly small, sparsely distributed populations between Point Hueneme and Point Conception, and only a few large populations in Santa Monica Bay. Studies of the nearshore benthos in these areas have not reported *Dendraster* (Hartman, 1956; Barnard and Hartman, 1959). In our experience, these regions are generally more protected than the rest of the southern California coast. Thus, in terms of adult density, the most "favorable" habitat for *D. excentricus* occurs off relatively exposed beaches of southern California.

Geographic Distribution and Age

Small juveniles are far more widespread than adults, which tend to be more aggregated and localized in their distribution. Although we usually found small juveniles with adult populations, the reverse was often not true. Indeed, Hartman *et al.* (1960), and Barnard (1963) listed "juveniles" of *Dendraster* sp. as one of the most abundant macroinvertebrates on inshore sandy bottoms of southern California. Juvenile and adult sand dollars in this habitat differ markedly in their feeding behavior: juveniles are buried or flat on the sand surface whereas most adults are inclined.

Bathymetric Distribution and Size

Mortensen (1948) claimed that the bathymetric range of *D. excentricus* is from shoreline to 55 m. Clark (1948) extended this range to 91 m but stated that most individuals do not occur below about 36 m. Some of the early records were no doubt based on *Dendraster laevis* Clark (1948), which also inhabits some coastal inlets, but generally occurs in deeper water than *D. excentricus.* For example, Johnson and Snook's photograph (1927: Fig. 196) labeled as *D. excentricus,* clearly represents *D. laevis.*

As noted above, the size of *D. excentricus* decreases in water deeper than about 9 m. Raup (1958) also noted that specimens of *D. excentricus* from deeper water are small. This relationship has been observed from southern California (Olga Hartman, Allan Hancock Foundation, pers. comm.), northern California (John De Martini, Humboldt State College and Jack Pearce, Sandy Hook Marine Laboratory, unpub. data) and Oregon (McCauley and Carey, 1967; J. A. Macnab, pers. comm.). These small, deep-water adults are very abundant. Clark (1948) reported that small *D. excentricus* comprised over 38% of all echinoids dredged in the eastern Pacific between 1931 and 1941 by the Velero III of the Allan Hancock Foundation. He referred to these small *D. excentricus* as "young" individuals. However, it is doubtful that the small size of deep-water sand dollars is necessarily indicative of age. To account for an observed "age" distribution, one might postulate that sand dollars in deeper water experience a heavy mortality, and that survivors migrate shoreward, but these possibilities find no support from our observations. To the contrary, the only migration of small sand dollars that we noted was that of juveniles moving out from the shoreward edge of the near-shore populations. Considering the great abundance of these small deeper-water adults, compared to large adults close inshore, it seems likely that they simply do not attain the larger size under condtions prevailing in deeper water.

Recent work with sea urchins (Leighton *et al.,* 1966; Ebert, 1968) has suggested that although relative food availability can be a limiting factor on population biomass, it is often expressed in the size, rather than the numbers of individuals. On this basis, one might predict that available food for *D. excentricus* off the outer coast is maximum just seaward of the breaker line, where the water is about 10 m deep, and that beyond this, available food decreases with depth.

THE PROBLEM OF ECOLOGICAL RACES

The distinctive characteristics of *D. excentricus* populations from the different habitats have led some investigators to postulate the existence of separate species, or intraspecific varieties. MacGinitie and MacGinitie (1968: p. 239) stated, ". . . judging from their habits, we believe there is no doubt that these two forms (outer-coast and coastal-inlet forms) are separate and distinct species of animals." Although biometric analyses have revealed differences in morphology between coastal-inlet and outer-coast sand dollars (Raup, 1956), the significance of such differences is questionable (Kelley, 1965). Furthermore, where populations are contiguous between a coastal inlet and the outer coast, individuals exhibit behavioral and phenotypic (Merrill, unpubl. data) intergradations. MacGinitie and MacGinitie (1968) found no such transitional populations, but we observed them at Estero de Punta Banda (loc. 2), Mission Bay (loc. 6) and Morro Bay (loc. 30).

It seems unlikely that an effective genetic barrier exists between proximate populations in different habitats, particularly in view of larval dispersion (Raup, 1956, 1958). The possibility of asynchronous reproductive cycles has not been investigated. Nevertheless, we will regard all populations of *D. excentricus* within our study area as comprising a single taxonomic entity until evidence to the contrary is more convincing. In addition, we believe that the pooling of coastal-inlet populations and outer-coast populations into two ecological races, as suggested by Raup (1956), may also be misleading. For example, at least in terms of feeding and other behavior, differences between bay and tidal-channel forms are greater than those between the latter and protected outer-coast forms. We conclude that *D. excentricus* possesses a phenotypic, behavioral and ecological plasticity like that observable in other echinoid species (*e.g.*, Lindahl and Runnström, 1929; Moore, 1935; Hagstrom and Lonning, 1961; Nichols, 1962; Lohavanijaya, 1965; Buchanan, 1966; Ebert, 1968).

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